

51. Reversible and Irreversible Evolution ; a Study based on Reptiles. By Dr. FRANCIS, Baron NORCSA.

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(Text-figures 8 & 9.)

The great amount of information that we have about the evolution of some groups of reptiles, the great amount of variability that these animals show, the long span of time that the history of their evolution covers, seem to make it advisable to base an investigation of the laws of evolution on the history of these groups. Fejérváry was one of the first who worked on these lines (6).

As is well known, in the skeletal structure of Reptilia many characters occur that show what has been called the irreversibility of evolution. Such characters are: the development of a secondary armour in *Dermochelys* (4), the changes in the pelvis of the orthopodous Dinosaurs (5), the secondary growth of the plastron in the Cinosternidæ (9), and the development of a new element (præpubis) functioning as pubis in the Crocodylia. Apart from these changes, some of which have been well studied, one can detect other less well-known changes tending to prove that sometimes a reversal of evolution can take place. Changes of this sort are: the secondary elongation of the anterior limbs in Dinosaurs, the development of the postorbital bar in Mammals and theromorphous reptiles, the redevelopment of more or less plate-like ventral pelvic elements in different reptiles, the occurrence of polygonal flat carpal and tarsal bones in highly specialised reptiles, and the relationship of the frontal to the orbit in different groups.

The aim of this paper is to give a description of the different changes of this second type and to draw conclusions.

§ (1) *The elongation of the anterior limbs in specialised Dinosaurs.*

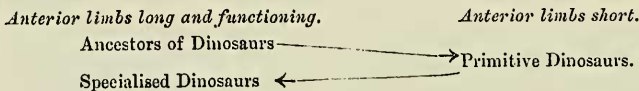
In all primitive diaptosaurian reptiles, such as Rhynchosaurians and Parasuchians, and in a less marked degree in the true Rhynchocephalians, the anterior limbs are generally only a little shorter than the posterior. These animals are exclusively quadrupedal. In the short-necked Ornithosuchians and in the long-necked Proterosaurians, which were partly bipedal, a marked shortening of the anterior limbs can be detected. This shortening is stronger in the originally bipedal Dinosaurs. It is very noticeable in the lightly-built triassic carnivorous Dinosaurs (*Podokoosaurus*, *Hallopus*, *Procompsognathus*) but less marked in the jurassic and cretaceous representatives of this group. In *Procompsognathus* (and *Podokoosaurus*?) the ratio

of the anterior limb to the posterior is 10/27, in the jurassic *Compsognathus* 10/18, in the nearly contemporaneous *Ornitholestes* 10/15, and in the cretaceous *Struthiomimus* 10/16. In this group, in which not the jaws or the posterior limbs but the anterior limbs were used for seizing the prey, a decided lengthening of the anterior limbs occurs. In the heavily-built carnivorous Dinosaurs, in which, much as in the birds of prey, a prehensile foot is developed, this elongation does not occur and the anterior limbs remain small or almost vanish (10).

A relatively short anterior limb is also met with in all bipedal orthopodous Dinosaurs. The ratio is 10/21 in *Hypsilophodon*, 10/23 in *Thescelesaurus*, 10/19 to 10/17 in *Camptosaurus*, 10/14 in *Iguanodon*, 10/17 in *Kritosaurus*, and 10/15 in *Corythosaurus*. Though less clearly than the preceding one, this list also shows that in the more specialised forms, as *Iguanodon* and *Corythosaurus*, the anterior limbs are a trifle longer than in the more primitive forms.

In the quadrupedal Sauropoda the anterior limbs are mostly shorter than the posterior; in one group, however, the Brachiosauridae, the length of the limbs is nearly equal. In this case the secondary elongation is very marked (10).

All these data show that in those specialised Dinosaurs in which the anterior limb is continuously used a secondary lengthening of this part occurs. This can be considered as a reversal to the ancestral pro-dinosaurian type. Diagrammatically these changes can be expressed in the following manner:—



For one reason the case is not quite conclusive, for it can be surmised that the apparent secondary elongation is not due to a renewed growth but simply to the fact that in Dinosaurs the posterior limbs, on account of their being more used, grew big first, and that the growth of the anterior ones set in later. Since also such a hypothesis might explain the temporary disproportion of the limbs, the case must be considered doubtful.

§ (2) *The development of the postorbital bar.*

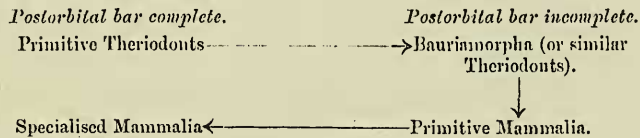
The second case to be dealt with is more typical than the first. While in all more or less primitive reptiles the postorbital bar is complete, it is open in some rather specialised forms. Such Reptiles are: many snake-shaped reptiles, some other lacertilians, and the Bauriamorpha. Contrary to what is known in Reptiles, in Mammals the postorbital bar is incomplete in the primitive forms and complete only in the younger Equidae, most of the Artiodactyla, and in the Primates. This being the case, it may be concluded that all Mammals descended from animals lacking a postorbital bar.

In spite of many mammalian characters, such as the structure of the teeth, the articulation of the lower jaw, and the shape of the brain, not the Cynognathidæ but the Bauriamorpha must be considered as the ancestors of the Mammalia, for the ribs of the former show a non-mammalian trend of evolution. Curiously enough the Bauriamorpha have no postorbital bar. Thus the disappearance of this part in the Bauriamorpha and its reappearance in the higher mammals again points towards a reversal. Wortmann's discoveries of a separate postfrontal and even of a postorbital bar in some Insectivora (19) show that this part of the mammals is not analogous but homologous with the same part in reptiles.

This change seems again to be nothing else than the retention of an embryonic character in the adult, for frequently in embryos of animals characters appear that are later reduced. Good examples are afforded by the temporary development of a third cervical rib in the Lacertilia (8) and by the development of a fourth and fifth digit in embryos of birds (13).

A process similar to that which accounts for the development of the postorbital bar in higher mammals is evidently also changing the development of the claws in *Opisthocomus*, for this bird is evidently forgetting how to fly and learning how to climb (10).

For the history of the development of the postorbital bar in Reptiles and Mammals the following diagram can be drawn:—



§ (3) *The development of the ventral elements of the pelvis.*

As is well known, in primitive Stegocephalians, for example the Branchiosauridæ, the ventral elements of the pelvis consist of four, or sometimes even only of two, small disk-shaped centres of ossification that were evidently embedded in a large plate of cartilage. Much the same type of pelvis is found in the recent Urodeles. In the more specialised Stegocephalians (*Eryops*, *Cacops*) the two ventral elements form a continuous mass of plate-like bone with a small foramen perforating each pubis. It is evident that this type of pelvis originated in the complete ossification of the whole cartilage of the more primitive forms. This solid type occurs also in the Cotylosaurians (*Seymouria*, *Diadectes*, *Labidosaurus* (text-fig. 8 (1)), *Pareiasaurus*); in the most agile Cotylosaurians (*Procolophon*), however, and in the Pelycosaurians (*Ophiacodon*, *Varanosaurus*) a central perforation and separation of the pubis and ischium appear. From this latter type were evolved the pelvises of the higher reptiles, that show either one great perforation in the centre and two small foramina obturatoria passing through the pubes, or one large

foramen on each side between each pubis and ischium (text-fig. 8 (2)). Through this foramen the obturator nerve passes. As these openings grow larger the central pelvic elements are more or less reduced to rod-like bones. This change is analogous to the one that occurs in the skulls of different groups of reptiles, for also in these the originally plate-like skull bones are reduced, where they do not cover the brain-case, to rods that correspond to the different lines of stress and strain.

The tendency to develop more or less rod-like ventral pelvic elements is fairly well indicated in most tortoises (text-fig. 8 (3)), with the exception of the marine ones, for the median ossification is less marked in the modern tortoises than in the Amphichelydæ. The same structure is also observable in the primitive Sauropterygians (*Neusticosaurus* (text-fig. 8 (5)), *Anarosaurus*).

Among the Parapsida the rod-like pelvis is still missing in *Areoscelis* but clearly indicated in *Pleurosaurus* and well developed in all Squamata. Among the Rhynchocephalians large ventral pelvic openings are absent in *Howesia* and the Rhynchosaurians, but they are well developed in all other Rhynchocephalians (text-fig. 8 (7)) with exception of the Proganosauria. In all Thecodontia, all Dinosaurs, and all Crocodiles the pelvic apertures are always large.

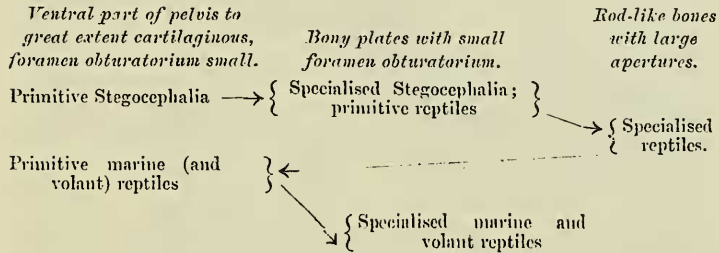
In contrast with this more or less plate-like ventral pelvic elements are to be found in the specialised Sauropterygians (text-fig. 8 (6)), in the Proganosauria (text-fig. 8 (8)), and in the Pterosaurians. Among the latter this feature is very noteworthy, for it is especially well developed in the Pteranodontidæ, which are the most specialised members of the Order (text-fig. 8 (9)).

Dermochelys, which is derived from some unknown chelonian tortoise, has much smaller foramina obturatoria than all the Chelonidæ, and retains in the pelvis a great amount of cartilage throughout life (text-fig. 8 (4)). In this respect the pelvis of an adult *Dermochelys* recalls somewhat the pelvis of *Hatteria* in an early stage of development (11, 14). The resemblance which Baur (1) detected between the pelvis of some Testudinata and the pelvis of the Rhynchocephalia is, of course, only due to a case of convergence, for the situation of the foramen obturatorium is different in the two groups.

Comparing now the relationships of the reptiles mentioned in the above lines, it becomes clear that in three cases plate-shaped pelvic elements must have arisen from rod-shaped bones. The Plesiosaurians must have arisen from Nothosaurian reptiles, the Proganosauria from jurassic Rhynchocephalians, and the Pteranodontidæ from triassic Thecodontia. Thus these three cases are quite characteristic cases of reversal. An indication of the same sort of reversal is afforded by the differences that separate *Dermochelys* from the Chelonidæ. These differences show more clearly than the return of the postorbital bar in what manner such a reversal begins. As suggested in the former case, it starts by the retention of an embryonic stage throughout life.

Supposing that in *Dermochelys* the whole of the cartilage were to turn to bone, very soon a pelvis would evolve that would recall the most primitive reptilian pelvis. It would be more primitive than the pelvis of the Amphichelydæ. That such a reversal can actually take place will be proved in detail in the following paragraph, here it is enough to emphasise that in *Pteranodon* such an ossification actually did occur.

On account of the complexity of the changes in the ventral elements of the pelvis of reptiles the diagram also becomes complex.



§ (4) *Carpus and tarsus of reptiles.*

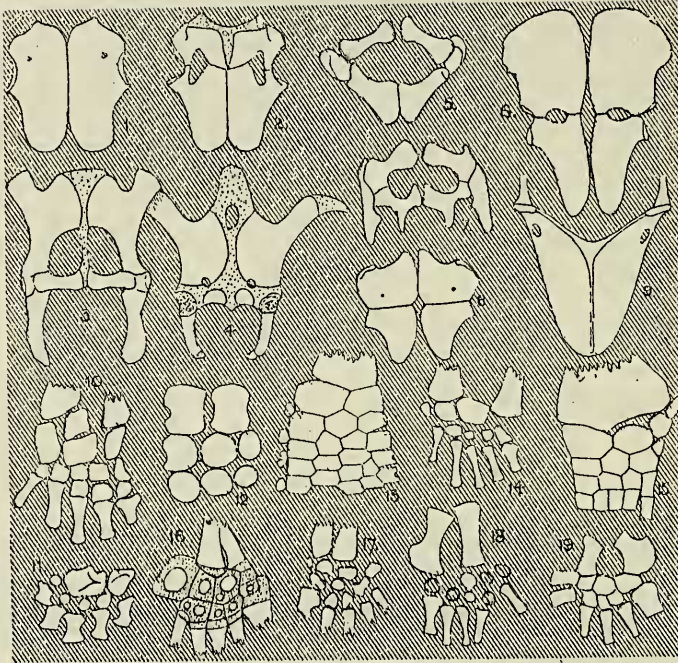
The changes that can be observed in the carpus and tarsus of reptiles are similar to those in the pelvis.

In primitive Stegocephalia, as in modern Urodeles, the carpus and tarsus consist of flat polygonal pieces of cartilage with small disk-shaped ossicles in their centre. In this respect it is sufficient to refer to *Uranocentrodon* and to *Scincosaurus*, the foot-bones of which have been figured by Broom (3). In other more reptile-like Stegocephalians carpus and tarsus consist no longer of cartilage but of more or less flat polygonal bones with but little cartilage between them (text-fig. 8 (10)) (*Trematops*). These tarsal and carpal bones evidently originated by the ossification of the whole or of nearly the whole cartilage of the primitive forms without much change in shape.

With the exception of the Procolophonidæ, the Cotylosauria show much the same sort of foot-bones as the Stegocephalia. In the primitive ones (*Diadectes*, *Disparaetus* (text-fig. 8 (11)), *Limnoscelis*), evidently polygonal cartilage plates were present with disk-like centres of ossification in their middle, while in the more specialised ones (Pareiasauridæ) the cartilage is replaced by polygonal bone. In the Procolophonidæ the structure of the foot-bones is different. Instead of cartilaginous or osseous, nearly immovable elements, ossicles with well-marked concave and convex surfaces of articulation are present. Probably a fair amount of cartilage was present, but probably also the surfaces of the cartilage-bodies were curved.

In the Pelycosaurians the carpus is still sometimes polygonal with a small amount of flexibility (*Ophiacodon*), sometimes rounded with a fair amount of cartilage (*Varanops*), and sometimes

Text-figure 8.



1. Plate-like pelvis of carnivorous primitive Cotylosaurian *Labidosaurus* (from Case).
2. Plate-like pelvis of carnivorous highly organised Theriodont *Cynognathus* (from Seeley).
3. Rod-shaped pelvis of moderately specialised marine tortoise *Chelone* (from Hofmann).
4. Cartilaginous plate-like pelvis of highly specialised marine tortoise *Dermochelys* (from Völker).
5. Rod-shaped pelvis of semi-aquatic Sauropterygian *Neusticosaurus* (from Fraas).
6. Plate-like pelvis of highly organised marine Sauropterygian *Peloneustes* (from Linder).
7. Rod-like pelvis of terrestrial Rhynchocephalian *Sauranodon* (from Lortet).
8. Plate-like pelvis of aquatic Rhynchocephalian *Chanpsosaurus* (from B. Brown).
9. Plate-like pelvis of highly specialised Pterosaurian *Pteranodon* (from Eaton).
10. Polygonal tarsus of highly specialised Stegocephalian *Trematops* (from Williston).
11. Disk-shaped cartilaginous tarsus of primitive Cotylosaurian *Disparactus* (from Case).
12. Disk-shaped carpus of primitive Ichthyosaurian *Delphinosaurus* (from Merriam).
13. Polygonal carpus of highly specialised Ichthyosaurian *Ichthyosaurus* (from Huene, referred to there under the generic name *Turypterygius*).
14. Disk-shaped carpus of primitive Sauropterygian *Proneusticosaurus* (from Volz).
15. Polygonal carpus of specialised Sauropterygian *Polycotylus* (from Williston).
16. Disk-shaped carpus of highly specialised marine tortoise *Dermochelys* (from Völker).
17. Spherical carpus of primitive marine tortoise *Toxochelys* (from Hay).
18. Disk-shaped carpus of primitive Mosasaurian *Tylosaurus* (from Osborn).
19. Polygonal carpus of specialised Mosasaurian *Platecarpus* (from Williston).

well ossified with spherical surfaces of articulation (*Dimetrodon*). The latter type is to be found also in all terrestrial Squamata that have well-developed feet. Very little is known until now about the foot-bones of the Theromorpha; they seem, however, always to have attained a high degree of perfection.

Turning from the monozygocrotaphous Theromorpha to the likewise monozygocrotaphous Sauropterygians, which evidently descended from Pelycosaurians or Theromorpha, one is surprised to remark that even in those Sauropterygians that are least adapted to aquatic life (*Neusticosaurus*, *Pronesticosaurus* (text-fig. 8 (14)) the foot-bones are flat and rounded ossicles that evidently formed the centres of cartilaginous, polygonal plates. The same sort of foot-bones are present in the liassic Plesiosaurians. In the more specialised later Plesiosaurians, instead of the cartilaginous plates, polygonal flat bones are present. The flat polygonal bones observable in *Elasmosaurus*, *Polycotylus* (text-fig. 8 (15)) or *Cimoliosaurus* recall somewhat the flat polygonal bones of the specialised Stegocephalians.

Similar changes as those in the Sauropterygians can also be observed in the Ichthyopterygians. In *Mesosaurus* and some triassic Ichthyosaurians (*Shastasaurus*, *Delphinosaurus* (text-fig. 8 (12)) round bony disks occur that were evidently surrounded by extensive cartilage. In all the more specialised Ichthyosaurians (text-fig. 8 (13)) polygonal bony plates are present. These are firmly applied against each other.

Somewhat similar changes as in these groups are to be met with in the Testudinata. In the terrestrial tortoises polygonal bones occur with a small amount of mobility between them. In the Trionychidæ these bones show by retaining at their angles a good amount of cartilage a tendency to round off these angles. In the Chelonidæ (text-fig. 8 (17), *Toxochelys*) this process is still more marked; finally, in *Dermochelys* (text-fig. 8 (16)) instead of angular bones, polygonal plates of cartilage are present, with flat bony disks in the centre. These changes show that the rounding off of the primitive polygonal foot-bones of the Testudinata is due to the retention of an embryonic stage throughout life (14).

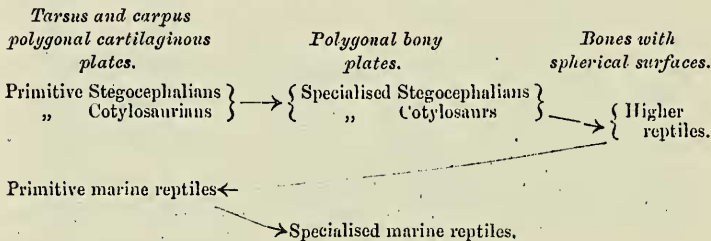
Applying this observation to the fossil marine forms hitherto discussed, it becomes obvious that also in these first a cartilaginous embryonic stage, with small centres of ossification, had become permanent for some time, and that after this transitory stage extensive ossification set in, in much the same manner as in the most primitive reptiles. In this instance it will be remembered that the hypothesis of a secondary ossification has already been brought forward in the foregoing paragraph.

Among the marine Squamata the carpal and tarsal bones retain spherical articulating surfaces in *Opetiosaurus*, they have become to a great extent cartilaginous in *Tylosaurus* (text-fig. 8 (18)), and are already to some extent replaced by flat polygonal bones in *Platecarpus* (text-fig. 8 (19)). So also in this group the same changes occur as in the groups already dealt with.

Until the present investigation only the shape of each isolated foot-bone was dealt with, now it becomes necessary to consider the whole foot. While each separate foot-bone shows a decided reversal of evolution, the whole foot as such shows something else. Although several of the carpal and tarsal bones can be identified in all groups of reptiles, nevertheless the number and the relative position of the foot-bones continually change. This is why the foot of an Ichthyosaurian can readily be distinguished from the foot of a specialised Stegocephalian. In consequence of the foot-bones always being differently arranged in the different groups of reptiles, evolution seems to be irreversible.

Thus the foot-bones of reptiles show in a drastic manner how in one point of an organ the evolution can be reversible, but irreversible in another. When such a phenomenon occurs in correlated parts of the body, it is admissible to call the case a mixed one.

The diagram representing the evolution of the foot-bones of reptiles recalls the one of the evolution of the pelvis:—



§ (5) *The development of the supraorbital region.*

In nearly all the Stegocephalians the postfrontal and the prefrontal meet above the orbit and exclude the frontal from this opening. It is only in some highly specialised forms that exceptions to this rule can be found. First of all the frontal touches the orbit in those gigantic and, as Watson (15) proved, specialised forms, such as *Capitosaurus*, *Mastodonsaurus*, and *Cyclotosaurus*; secondly, this occurs in those Labyrinthodonts that show a very marked broadening of the skull, such as *Plagiosaurus* (text-fig. 9 (4)); thirdly, this occurs in the aberrant Microsaurian *Diplocaulus* (text-fig. 9 (2)). In the less aberrant relatives of *Plagiosaurus* and *Diplocaulus* as, for example, *Batrachosuchus* (text-fig. 9 (3)), *Diceratosaurus*, and *Batrachiderpetum* (text-fig. 9 (1)), the frontal is yet excluded from the orbit.

Other Stegocephalians, in which the frontal likewise borders the orbits, are *Gephyrostegus*, which is characterised by the thinning out of the cranial roof, suggesting the formation of temporal vacuities, and *Trematops* and *Broiliellus*, that both recall the Cotylosauria. From all this it becomes evident that in the Stegocephalia the entry of the frontal into the orbits is a sign of specialisation. For the sake of convenience one can call the type

where it enters into the orbit the *neo-orbital* type and retain the expression *palæo-orbital* for the other.

Among the Cotylosauria the Diadectidæ (text-fig. 9 (5), *Diadectes*), Pareiasauridæ, and Limnoscelidæ show the same structure as the primitive Stegocephalians, the Captorhinimorpha and the Procolophonidæ the other. *Procolophon* (text-fig. 9 (6)) is a very agile Cotylosaurian, showing also many other signs of specialisation: for example, a small lacrymal bone. In the Captorhinimorpha, on the other hand, the limbs are specialised to a rather high degree.

Among the Testudinata that are somewhat allied to the Cotylosaurians, the relation of the frontal to the orbit varies. In some primitive Testudinata, such as *Triassocheilus*, *Chisternon*, and *Kallokibotium*, the palæo-orbital type is preserved; in some other Amphichelydæ already the neo-orbital type occurs. Curiously enough, the palæo-orbital type occurs also in the Protosteginæ and the Dermochelydæ (text-fig. 9 (8)), while the Lytolomidæ and the Chelonidæ (text-fig. 9 (7), *Toxochelys*) show the neo-orbital type. In primitive Chelonidæ (*Toxochelys*) and in the embryos of *Chelone* (14) the neo-orbital type is more marked than in the adult *Chelone*. In the rest of the Tortoises generally the neo-orbital type is met with; the palæo-orbital type occurs, however, in the Platysterninæ and Chelydridæ, and sporadically among the Emydidæ.

In *Platysternum*, *Dermochelys*, and some Chelydridæ, as *Macroclermys*, the palæo-orbital type is associated with a secondary enlargement of the bones forming the roof of the skull and with the loss of the power of hiding the head under the shield. In accordance with this, in *Dermochelys*, *Chelone*, and *Chelydra*, the posterior excavation of the parietal and the squamosal is more marked in the embryos than in the adult (14).

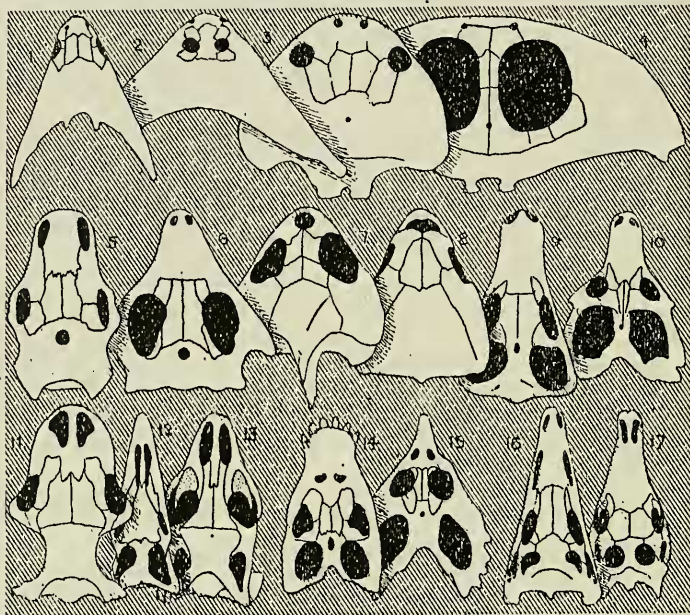
Considering that in the most primitive Tortoises the capacity of withdrawing the head had not yet been acquired, and that it was but secondarily lost in *Dermochelys*, *Chelone*, *Platysternum*, and *Macroclermys*, it becomes evident that this feature and the palæo-orbital type are connected with each other. Evidently the palæo-orbital type of the more specialised Tortoises has been developed from the neo-orbital type, for the ontogenetical changes observable in the Chelonidæ point in this direction.

Among the Theromorpha the neo-orbital type dominates *Microgomphodon* (text-fig. 9 (9)). The palæo-orbital type is only met with in the Cynognathidæ (*Protacmon*, text-fig. 9 (10)). In consequence of this it must be assumed that either the Cynognathidæ retained a very ancient structure, or that also in this case a reversal took place. Since in all Pelycosaurians that are ancestral to the Theromorpha the neo-orbital type likewise occurs, evidently the latter has to be assumed. As Pelycosaurians, it is quite enough to mention the genera *Varanosaurus*, *Sphenacodon*, *Theropleura*, and *Dimetrodon*.

Among the Placodontidæ, palæo-orbital genera as *Placodus*

(text-fig. 9 (14)) and neo-orbital genera as *Placochelys* (text-fig. 9 (15)) can be distinguished. Unfortunately nothing is known about the evolution of this group, therefore no conclusions can be drawn.

Text-figure 9.



1. Palæo-orbital skull of primitive Microsaurian Diplocaulidæ, *Batrachiterpeton* (from Watson).
2. Neo-orbital skull of specialised Microsaurian Diplocaulidæ, *Diplocantus* (from Douthitt).
3. Palæo-orbital skull of primitive Stereospondylous Brachyopidæ, *Batrachosuchus* (from Watson).
4. Neo-orbital skull of specialised Stereospondylous Brachyopidæ, *Plagiosaurus* (from Fraas).
5. Palæo-orbital skull of primitive Cotylosaurian *Diadoctes* (from Hheno).
6. Neo-orbital skull of specialised Cotylosaurian *Procolophon* (from Woodward).
7. Neo-orbital skull of primitive marine tortoise *Toxochelys* (from Huy).
8. Palæo-orbital skull of specialised marine tortoise *Dermochelys* (from Völker).
9. Neo-orbital skull of primitive higher Theriodont *Micromphodon* (from Watson).
10. Palæo-orbital skull of specialised higher Theriodont *Protacmon* (from Watson).
11. Palæo-orbital skull of Lepidosaurian *Heloderma* (from Phisalix).
12. Neo-orbital skull of Lepidosaurian *Platecarpus* (from Williston).
13. Tectorbital skull of Lepidosaurian *Varanus* (from Schmidt).
14. Palæo-orbital skull of Dranitesaurian *Placodus* (from Broili).
15. Neo-orbital skull of Dranitesaurian *Placochelys* (from Jüchel).
16. Neo-orbital skull of primitive Archosaurian *Euparkeria* (from Broom).
17. Tectorbital skull of specialised Archosaurian *Camptosaurus* (from B. Brown).

Among the Sauropterygians, the neo-orbital type is met with in *Anarosaurus*, *Pistosaurus*, and *Nothosaurus*, the palæo-orbital type in *Cymatosaurus* and all Plesiosaurians. In all the Plesio-

saurians the frontal shows a decided tendency to vanish altogether, and, besides this, in the more specialised long-snouted Plesiosaurians (the Pliosaurians) the tendency exists to develop large supraorbital bones. This tendency is well observable in the genera *Peloneustes*, *Brachyauchenias*, and *Trinacromerum*. In these genera the prefrontals and postfrontals are long and narrow bones. On account of the reduction of the frontal these animals revert at first to the palæo-orbital type, but when the broadening of the head sets in they develop on other lines.

In the Parapsida, that include the Areoscelia, the Acrosauria, and the Squamata, the frontal nearly always separates the prefrontal and the postfrontal. While it borders the orbit in *Areoscelis*, *Pleurosauros*, all primitive Chameleons (18) and many Lacertilians (*Platecarpus*, text-fig. 9 (12)), it is excluded in some Lacertilians from the orbit by a supraorbital bone (text-fig. 9 (13), *Varanus*). *Heloderma* (text-fig. 9 (11)) and the specialised Chameleons (17) differ from all the other Squamata in showing the palæo-orbital structure, but this may be due to a reversal. Thus in this group the structure varies.

In the Diaptosaurians (text-fig. 9 (16), *Euparkeria*), the Dinosaurs, and the Crocodiles, the prefrontals and the postfrontals never meet. In some Crocodiles however, and in the orthopodous Dinosaurs supraorbital bones are developed (text-fig. 9 (17), *Camptosaurus*).

For the neo-orbital type, in which a supraorbital bone is present, Fejérváry's term, *tectorbital* (7), can be adopted. Since the supraorbital bone is only developed in few groups of reptiles, the tectorbital type is evidently new.

Proceeding now to group the primarily palæo-orbital, the neo-orbital, the secondarily palæo-orbital, and the tectorbital types according to chronological order, it is soon seen that the primarily palæo-orbital types are either permian reptiles or such that are closely allied to permian reptiles. The neo-orbital type occurs in different groups from the Permian upwards, it is most marked in the most advanced reptiles; the secondarily palæo-orbital forms are found from the Trias upwards, but mostly among comparatively low posteretaceous reptiles; finally tectorbital types occur exclusively from the Jurassic upwards.

The average conclusion to be drawn is that in primitive reptiles (Cotylosauria, Tortoises) a reversal could easily occur from the neo-orbital type to the palæo-orbital type; that, however, in the more highly developed reptiles (Crocodiles, Dinosaurs) the broadening of the skull could no longer be attained by a reversal but only by the development of a new bony element. Comparatively primitive reptiles, as Sauropterygia and Squamata, seem to be intermediate between the two extremes. The primitive nature of the Squamata is best shown by the circulatory and respiratory organs.

In two most important papers Weidenreich (16, 17) pointed out that in some living animals characters occur that are very

characteristic and date back at least to Pliocene time, but that are all the same not yet perfectly fixed. Such characters have each time to be acquired by a special stimulus in every individual. When such a stimulus is lacking a reversal to the ancestral type takes place. Such characters are, for example, among many other ones, the blindness of *Proteus* (16) and the shape of the calcaneus in man (17).

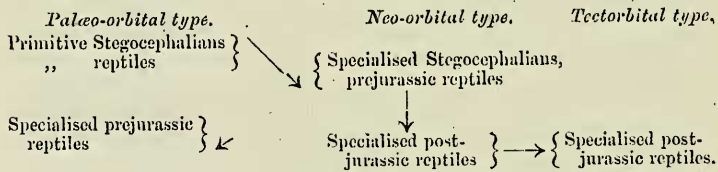
Other characters, as the development of the foramen of the operculum, through which, in the Urodela, the extremities are protruded (16), or the scrotum of man (16), are even then developed to a certain degree, when inciting stimuli, as the pressure of the extremities against the operculum or the descent of the testicles are not acting, but in such cases these characters are less marked than when the stimuli are acting.

A third group of characters is always developed in ontogenesis, and even apparently without reason. These observations show that in the fixing of new characters quite different stages occur.

Comparing now these stages with the changes found in the orbital region, it is evident that the reversal of the neo-orbital structure to the palæo-orbital type in permian or primitive reptiles (Tortoises) is entirely analogous to the case when a not yet fixed character is lost again. The undecided condition prevailing among the Sauropterygians and the Squamata can be well compared to the changes in Weidenreich's second group, and the development of the tectorbital type shows that in the highly developed reptiles the neo-orbital type had become fixed to such an extent that a reversal was no more possible.

In this way palæontological observations corroborate zoological research, and the interest of this case lays in that it is correlated with geological time.

The changes may be shown diagrammatically as follows:—



(The explanation of the abbreviated terms "prejurassic" and "postjurassic" is given in the text.)

CONCLUSION.

After having discussed five cases of reversible evolution, four of which are beyond question, and after having mentioned at the beginning of the paper several cases of irreversible evolution, conclusions may now be drawn.

The first certain case of reversible evolution shows how an ossification, which was interrupted during the course of evolution,

sets in again. The second case shows the persistence of a primitive stage of development in later more specialised forms, and shows the subsequent development of another stage of evolution through which the ancestral forms had passed long ago. The third case, the mixed one, shows a similar change coupled with "irreversible" evolution, and finally in the fourth case three phases can be discerned—one phase, in which a character is not yet fixed, so that a reversal is possible, a second undetermined phase, and a third, in which a reversal is impossible. In the latter case a particular function can only be attained by the development of a new organ.

Reviewing the "irreversible" cases, it can easily be detected that the apparent "irreversibility" is always due to the fact, that either an adjacent organ or an organ having a similar function is called upon to replace a degenerating organ or that in the absence of such parts a new organ is developed.

From the combination of these observations the following statements can be deduced:—

(1) An apparent irreversibility will occur when a certain character is already so strongly fixed that it cannot be altered. Such a fixation will occur all the sooner if the dismissed organ acquired a new function.

(2) An apparent irreversibility will occur when some function is not perfectly concentrated in a special organ, so that similarly functioning organs are ready at hand to replace each other.

(3) An apparent irreversibility will occur when an adjacent organ is ready to replace the more or less degenerated one. As an example of this sort the pelvis of the Crocodiles may be mentioned, for in this case the posterior ventral ribs assumed the function of the degenerated pubis and became the prepubes (new hypothesis of the author).

(4) Evolution will appear irreversible when in some organ the possibility of development still exists—*i. e.*, if the organ is yet in a primitive unspecialised state. In such a case this part is ready to develop new features that can replace another degenerating organ. An example of this case is afforded by the development of the secondary dermal armour in *Dermochelys*. As Schmidt's investigations (12) showed, the skin of the Tortoises is not yet strongly modified in the young, and so it has evidently not yet lost the general faculty of developing dermal ossifications.

When one of the four enumerated ways of solving a biological problem has become impossible, an animal can only be saved from extinction by a reversal to an embryonic stage. This will only be possible—

(1) if the state to be given up is not yet fixed by heredity. That means if this state is not very far back in the history. A good example is afforded by the development of the supraorbital region;

(2) if the embryonic state to be called upon has not in the meantime acquired a new and vital function. For this case

Salamandra atra is a good example, for if the gills of this Urodele were more adapted to the interuterine breathing than they actually are, the rearing of its larvæ in water would become impossible (16). Even in Tortoises evidently the embryonic gills are already modified to such an extent that the Mud-Tortoises were incapable of falling back on the use of their gills, and had in the course of their aquatic adaptation to develop new pharyngeal organs for breathing under water.

The unexplainable but important fact, that the life-history of each individual is always a distorted recapitulation of the history of its whole phylum, gives the clue by which we can understand why a limited reversal of evolution can occur.

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